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Evidence of repertoire sharing and stability despite a high turnover rate in a duetting neotropical wren

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In songbirds, the spatial pattern of song sharing among individuals is influenced by the song learning and dispersal strategies within each species. In birds where females and males sing and create joint acoustic displays (duets), the processes defining the patterns of song sharing become more complex as there might be different selection pressures shaping the behaviour of each sex. To provide further insight into the vocal development and the dispersal strategy of duetting tropical species, we investigated the patterns of individual and pair repertoire sharing, as well as the stability of these repertoires, in a colour-marked population of riverside wrens, *Cantorchilus semibadius*, located in the Osa Peninsula, Costa Rica. Using data collected over a five-year period, we found considerable variation in the sharing levels of phrase and duet type repertoires among neighbouring individuals coupled with a general decline of repertoire sharing as distance increased between birds' territories. These results are consistent with a pattern predicted in age-restricted learners that establish preferentially near their tutors. Furthermore, we found no evidence of individuals changing their phrase type repertoires over time, including after remating events. Duet type repertoires were also stable when pairs remained together. However, we observed a surprisingly high turnover rate. When individuals remated, even though the majority of the previous duet type repertoire remained, several new duet types were included. Taken together, our findings suggest that riverside wrens might create their individual repertoires by copying their same-sex parent and neighbouring individuals before dispersal. Additionally, we speculate that even though birds were able to create new duet types after changing partners, a substantial portion of their duet type repertoire might also be copied from their parents and neighbouring pairs during the initial critical period of song learning.

Keywords: duet type, phrase type, repertoire sharing, repertoire stability, riverside wren, turnover rate

Introduction

In many species of songbirds, individuals have repertoires of multiple song types which can be shared within and between populations, and which can be stable or change throughout their lives (Krebs and Kroodsma 1980, Catchpole and Slater 2008,

Byers and Kroodsma 2009). Within male songbirds, the spatial patterns of song sharing have been mainly attributed to the timing and length of the song learning period and the dispersal strategy followed by each species (Slater 1989, Beecher et al. 1994, Hughes et al. 1998, Beecher and Brenowitz 2005, Koetz et al. 2007, Vargas-Castro 2015). In fact, three distinctive spatial patterns of song sharing have been described, each resulting from different song learning and dispersal behaviours: a) high levels of song sharing and low variation among close neighbours combined with a rapid decline of song sharing with distance is predicted when individuals learn songs after dispersal or are open-ended learners and preferentially match the songs of their new neighbours, b) higher variation of song sharing among close neighbours combined with a general decline of song sharing with distance is predicted when individuals learn songs before dispersal and move short distances preferentially settling near their tutors and c) higher levels of song sharing at intermediate distances combined with low levels of song sharing at short and long distances is predicted when individuals are close-ended learners and preferentially settle where birds sing different songs or when individuals are open-ended learners and avoid singing shared songs with their close neighbours (Wilson et al. 2000).

In species where both females and males sing, mated birds often combine their individual vocalizations to create joint acoustic displays, also known as duets (Farabaugh 1982, Hall 2004, Hall 2009). Some of the most complex duetting behaviour has been found in species where each sex has a repertoire of sex-specific phrase types that they sing in coordination with their partner following a set of rules or a 'duet code' (Logue 2006). Pair-specific duet codes result in each pair within the population having a unique repertoire of duet types, which are consistent non-random associations of their individual phrase types (Logue 2006, Marshall-Ball and Slater 2008, Templeton et al. 2013, Rivera-Cáceres et al. 2016). In these species, the processes defining the patterns of song sharing become more complicated as there might be different selection pressures shaping the behaviour of each sex (Hall 2009, Rivera-Cáceres and Templeton 2017). For example, in canebrake wrens, *Cantorchilus modestus zeledoni*, females show a considerably smaller degree of variation in the phrase types they share with their neighbours than males do (Marshall-Ball and Slater 2008). Such discrepancy could be due to females dispersing closer to their natal territories or to both sexes learning their songs after dispersal with males having a bigger pool of tutors (Marshall-Ball and Slater 2008). Therefore, investigating the patterns of repertoire sharing between same-sex individuals and between pairs, together with the stability of these repertoires over time and after mate changes, provides valuable information on the vocal development and dispersal strategy of females and males of duetting species.

To date, several studies have found that individual phrase type repertoires are highly stable over consecutive years, even when birds change partners (Wickler and Sonnenschein 1989, Levin 1996, Grafe et al. 2004, Rogers 2005, Logue 2006, Rivera-Cáceres et al. 2016). These findings suggest that duetting birds might acquire their individual repertoire during early development as juveniles and that it remains fixed throughout their lives. A couple of studies that have focused on pairs that remained together across years have also found that duet codes are stable (Rogers 2005, Logue 2006). However, when individuals change partners, the few studies available show contrasting results. Whereas tropical boubous, *Laniarius aethiopicus*, always associate the same phrase type of their repertoire to the same known opposite-sex phrase type of the new mate (Grafe et al. 2004), in bay wrens, *Thryothorus nigrapillus,* and canebrake wrens, duet codes are flexible and individuals can create new duet types after being experimentally forced to change partners (Levin 1996, Rivera-Cáceres et al. 2016).

Even though duetting has been regularly associated with long-term partnerships (Farabaugh 1982, Benedict 2008, Hall 2009, Logue and Hall 2014, Tobias et al. 2016), divorce and mortality rates have been scarcely reported in most duetting species (Hall 2009). Investigating life history traits in duetting birds is central to our understanding of how coordinated signalling evolved to serve a variety of adaptive functions, including territory defence, mate location and mate guarding behaviour (Hall 2009). For example, in species presenting pair-specific duet codes, it has been shown that individuals require time to learn how to temporally coordinate and associate their individual phrases together (Marshall-Ball et al. 2006, Hall and Magrath 2007, Rivera-Cáceres et al. 2016). Thus, it has often been assumed that these species must have pair bonds that last for several years (Marshall-Ball et al. 2006, Benedict 2008, Hall 2009). However, in one of the few studies reporting pair bond length, Levin (1996) found that although bay wren pairs had on average 40% of pair-specific duet types, only 62% of pairs remained together more than a couple of months after the beginning of the breeding season. Having a high proportion of pair-specific duet types is, therefore, apparently not related to having long-term partnerships in this species, raising the question of how pair-specific duet codes evolved in bay wrens. More studies on colour-marked populations of duetting birds are needed to understand if pair-specific duet codes are associated with longer pair bonds, to investigate the benefits of learning such a highly coordinated display, and to understand the ecological conditions that have led to the evolution of this complex acoustic behaviour.

We monitored and recorded a colour-marked population of the neotropical riverside wren, *Cantorchilus semibadius*, over a five-year period to provide further insight into the vocal development, dispersal behaviour and life history traits of females and males in duetting species. Riverside wrens constitute a good study system as both sexes have repertoires of sex-specific phrase types that are combined to form highly complex and precise antiphonal duets that follow specific duet codes (Mann et al. 2009). First, we investigated the association between the levels of phrase and duet type sharing and the distance between birds' territories.

We predicted increasing levels of song sharing with decreasing distances between territories assuming that high levels of song sharing between neighbouring birds favours more effective counter singing dynamics, such as song type matching or repertoire matching. Second, we examined phrase and duet type repertoire stability in birds that remained together for two or more years and in birds that experienced natural mate changes. We predicted high stability in the phrase and duet type repertoires when individuals remained together given the strong evidence found in other duetting species to date. However, we predicted changes in duet codes in individuals who remated since new mates were expected to have different individual repertoires, which could drive the formation of new duet types. Third, we quantified individual turnover rates and pair-bond length in this population to investigate how these factors might influence duetting behavior. We predicted low individual turnover rates and stable pair-bonds would be observed since riverside wrens are a tropical species with year-round territories and pairs are known to have pair-specific repertoires of duet types.

Material and methods

Study species and study site

The riverside wren is a neotropical songbird that occurs on the Pacific slope of southern Costa Rica and in the Chiriqui province of western Panama (Skutch 2001). This species occupies dense vegetation in forest edges and alongside rivers where it forages exclusively for invertebrates in the forest canopy and understory (Skutch 2001). Riverside wrens are socially monogamous and nest throughout the year, remaining with their offspring for several months (Skutch 2001).

Riverside wrens have three different types of phrases that compose their duets: an introductory phrase (I) produced by the male, a female song phrase (F), and a male song phrase (M) (Mann et al. 2009), with the duet taking the form I (F M) *n*, with *n* being the number of cycles of the duet (i.e. the number of times the female and male phrases are alternated) (Fig. 1). When birds duet, the male often starts singing the introductory phrase, followed by the female's reply initiating a sequence of alternating phrases by the female and the male (on average 7–12 phrases per sex per duet) (Mann et al. 2009). However, I phrases are not always produced in duets, with duets also initiated with F or M phrases. Here we focus on the F–M phrases. Both sexes select from a repertoire of sex-specific F and M phrases both to perform solo songs and contribute to duets (Mann et al. 2009). When performing duets, the pair follows a duet code (Logue 2006), in which one or both individuals select a particular phrase type according to the partner's choice. Pairs sing with eventual variety, often repeating the same duet type multiple times before switching to another duet type (Mann et al. 2009).

We conducted observations and recordings of 37 pairs (61 individuals) in 23 territories within a population of riverside wrens for four years during a five-year period (2013, 2015–2017) between April and June at Osa Conservation's Piro field station (Fig. 2). The station is in lowland and wet rainforest at the Osa Peninsula in southern Costa Rica (8°24′6.96″N, 83°20′10.74″W). Riverside wrens are common in the study site, especially next to rivers and wetlands. We mapped the territories' boundaries with a hand-held global positioning system (Garmin GPS-60SCx, Garmin, Olathe, KS, USA). In several territories, individuals were replaced between field seasons, leading to data being collected on different pairs at the same geographical territory.

Data collection

Sound recordings were collected using a Sennheiser ME66 directional microphone and a Marantz PMD670 solid-state digital recorder (Recording format PCM-16, sample rate 44.1 k at 16-bit quantization). Recordings were made during the morning and evening hours, when birds have higher vocal activity, between 5 and 10 am and between 3 and 5 pm, respectively. Birds were recorded in natural context and while playback of riverside wrens' duets was broadcast to stimulate the focal pair to increase their singing rate. Often, these last recordings were made while conducting experiments to test hypotheses other than those addressed here (Quirós-Guerrero et al. 2017).

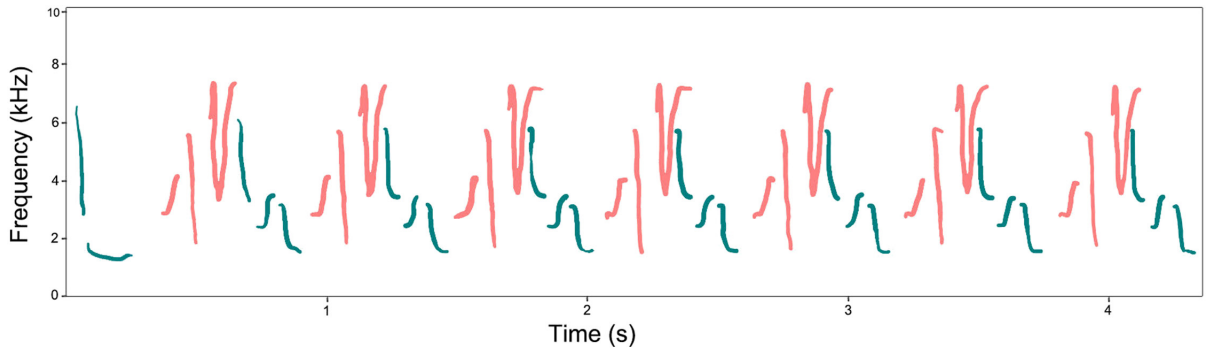

Figure 1. Spectrogram of a riverside wren duet type. The male contribution is depicted in teal and includes an initial introductory phrase (I phrase) and the male sex specific phrase (M phrase). The female contribution is depicted in coral and includes a female sex specific phrase (F phrase).

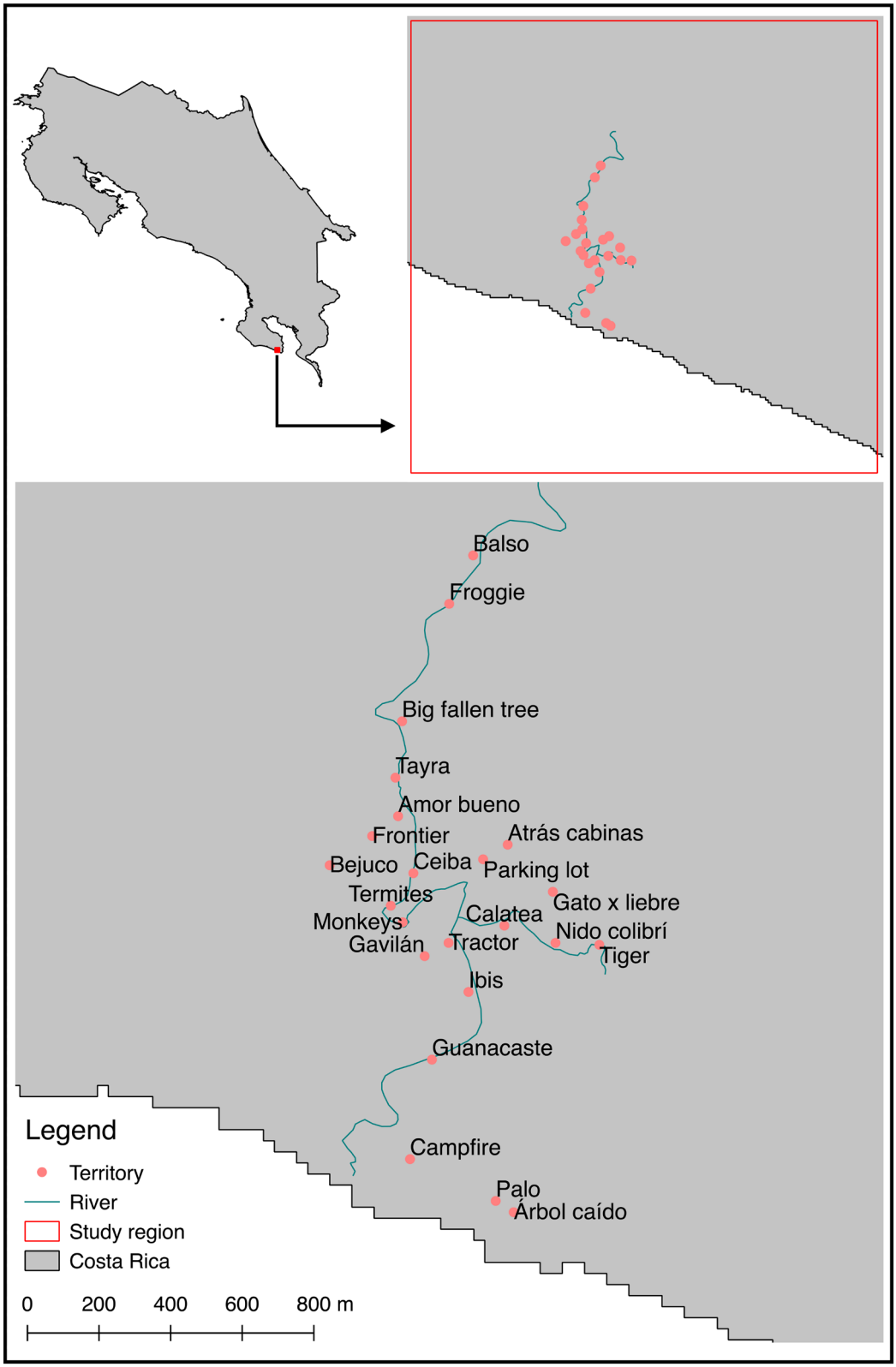

Figure 2. Map of the study site in Osa Peninsula, Costa Rica, with 23 riverside wren territories where we monitored and recorded 37 riverside wren pairs during 2013–2017. 17 territories were established next to one of the two main rivers at the field station and the remaining 6 territories were established in wetlands.

Phrase and duet type classification

We analyzed more than 600 h of field recordings. From these, we isolated all phrase and duet types using Syrinx (J. M. Burt, Seattle, Washington, USA) with a Hanning window, a 512 pt FFT, and a temporal resolution of 5.8 ms. We created sound spectrograms and a library of phrase types for each individual and a library of duet types for each pair; all songs were categorized based on visual inspection (Nowicki and Nelson 1990, Templeton et al. 2013, Rivera-Cáceres et al. 2016). A subset of the data (60 duets, i.e. 60 male phrase types and 60 female phrase types) was also categorized by a second observer to assess the level of inter-observer reliability. The second observer was given the library of phrase types obtained by the first observer and asked to assign the subset of phrases according to the library. Only 10 out of 120 phrase types were categorized differently between observers, resulting in a reliability score of 91.67%.

Repertoire size estimation

Given that rare phrase types and rare duet types are less likely to be sampled, complete repertoires were difficult to obtain. As a result, an asymptotic estimation approach to infer phrase/duet type richness, i.e. the number of different phrase/duet types in a repertoire, was adopted. In particular, we used the Chao-1 index (Chao et al. 2014), a non-parametric estimator for abundance data, which in the case of this study corresponds to the number of times each phrase/duet type was recorded. Additionally, we obtained rarefaction and extrapolation sampling curves to assess the sampling effort needed to obtain asymptotically complete repertoires (Fig. 3). These analyses were computed using R 3.1.0 software (<www.r-project.org>), using package iNEXT (Chao et al. 2014, Hsieh et al. 2018). Females tended to have smaller repertoires than males and asymptotes were reached at higher effort levels for duet types, as both females and males were consistently seen linking a phrase type of their own with more than one phrase type of the opposite sex. Although some phrase types were used to create more than one duet type, the duet types were repeatable and therefore consistent with the pair's duet code.

Repertoire sharing

Repertoire sharing of female phrase types, male phrase types and duet types was quantified using the song sharing index, $S = 2N_s/(2N_s + a + b)$, in which N_s is the number of shared phrase/duet types between two individuals/pairs and a and b are the non-shared phrase/duet types of each individual/pair (McGregor and Krebs 1982). Females were included in this analysis only if we had recorded ≥ 20 different phrase types

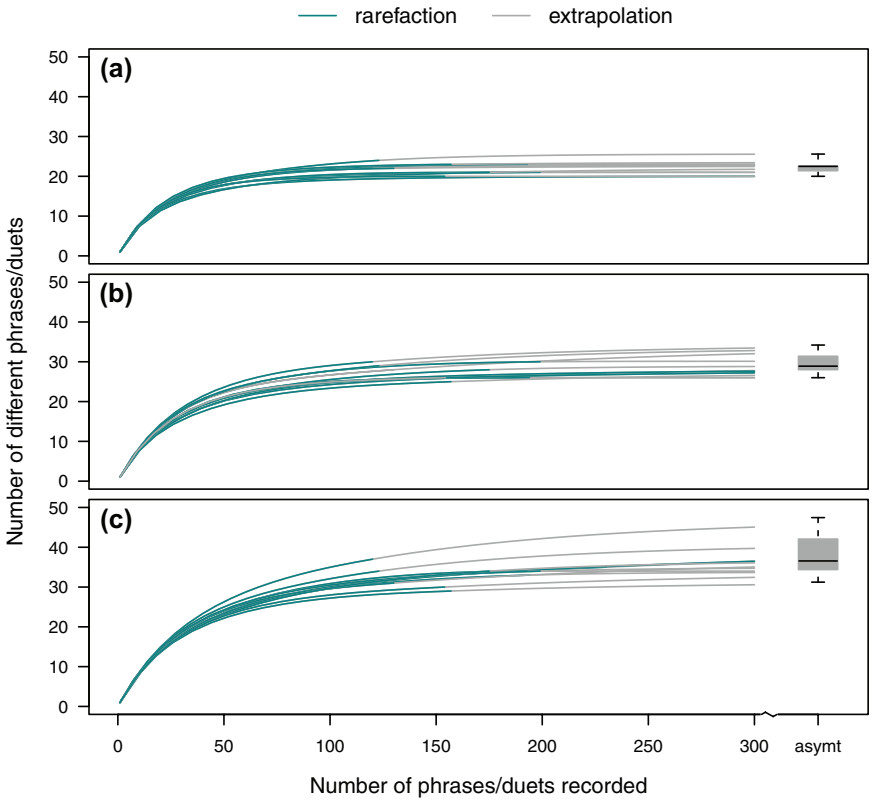

Figure 3. Cumulative curves of different (a) female phrase types, (b) male phrase types and (c) duet types according to the number of phrases/duets recorded in the songs of 11 pairs (11 females, 11 males) of riverside wrens. Rarefaction values are the actual recorded phrase types/duet types and extrapolation values are the estimated full repertoire sizes.

in their repertoires (22 females throughout 2013–2017), males if we had recorded ≥ 22 different phrases types (28 males throughout 2013–2017), and pairs if we had recorded ≥ 27 different duet types (24 pairs throughout 2013–2017). These criteria were based on the cumulative curves of phrase and duet types plotted against recording effort (number of recordings) that showed that this was close to the point at which new phrase/duet types' discovery rates approximately levelled off (Fig. 3). We also obtained an estimate of average song sharing across the population by calculating the average sharing between one focal individual/pair paired with every other same-sex individual/pair each year, and then averaging the results over all focal same-sex individuals/pairs.

To investigate the relationship between the degree of song sharing and the distance between territories, we performed permutation-based Mantel tests, which assess the correlation between matrices of song sharing (song sharing coefficient, *S*) across territories and the corresponding matrices of the geographical distance between them. Distances were measured in meters between territories' centres. A two-sided p-value was evaluated using 1000 permutations of rows and columns of the sharing matrix. We only included in this analysis the three years in which we had 10 or more territories with complete or near complete repertoires of phrase and duet types (2015, 2016, 2017). These analyses were conducted using R 3.1.0 software (<www.r-project.org>), using package ncf.

Repertoire stability

Phrase and duet types stability were also assessed based on Chao-1 index estimates of phrase and duet types richness (number of different phrase/duet types in a repertoire). Given that in many cases we could not obtain complete repertoires, this asymptotic estimator is particularly useful as it estimates repertoire sizes that would have been observed if infinite duets had been recorded. Stability was assessed: 1) within pairs across years; and 2) across pairs within territories. Stability across years 1) was evaluated when individuals remained together, whereas stability across pairs 2) was evaluated when individuals experienced natural mate changes. Reference years and pairs were defined for comparison purposes, to test stability across years and across territories, respectively. For these references, asymptotic estimators of phrase/duet type richness (repertoire sizes), as well as the corresponding 95% confidence intervals, were obtained. For the remaining years/pairs, i.e. those compared to the reference years/pairs, the number of different phrase types and duet types recorded that were not recorded in the reference were registered. Additions to the estimated reference repertoire that exceeded the upper 95% confidence interval of the Chao index were considered to be evidence of a change in individuals and pairs repertoires and, therefore, lack of stability. These analyses were computed using R 3.1.0 software (<www.r-project.org>), using package iNEXT (Chao et al. 2014, Hsieh et al. 2018). Following the previously defined criteria based on cumulative curves, only pairs with complete or nearly complete repertoires were included in this analysis. As a result, 11 pairs were considered in the analysis for individuals that remained together in the same territory and 8 pairs were considered in the analysis for individuals that changed partners.

Turnover rates and pair-bond length

Banded individuals were re-sighted between 2013 and 2017. Both individual IDs and location (territory) were continually surveyed across and within years, allowing the quantification of pair-bond duration and annual turnover rates.

Results

Repertoire size

Average estimated repertoire sizes were: 22 phrase types (20–25, 95% CI) for females (n = 22), 28 phrase types (24–32, 95% CI) for males (n = 28) and 35 duet types (30–43, 95% CI) for pairs (n = 24). On average, females had 0.31 ± 0.01 unique phrase types, males had 0.67 ± 0.02 unique phrase types, and pairs had 4 ± 0.03 unique duet types in their repertoires. Across the entire population, we found a total of 41 female phrase types, 80 male phrase types and 249 duet types. Of these, 10 female phrase types, 24 male phrase types and 124 duet types were unique to a single individual/pair in the population.

Repertoire sharing

Across the population, females shared 80 ± 0.01% (SE) of their phrase types, males shared 59 ± 0.01% of their phrase types and pairs shared 32 ± 0.01% of their duet types, when averaging pairwise comparisons with all other individuals/pairs included. In comparison, phrase and duet type sharing were, on average, higher between immediate neighbouring birds: females shared 86 ± 0.02% of their phrase types, males shared 67 ± 0.02% of their phrase types and pairs shared 48 ± 0.02% of their duet types. However, there was considerable variation amongst immediate neighbours with birds sharing 73–95% of female phrase types, 47–87% of male phrase types and 24–65% of duet types (Fig. 4). Finally, the degree of phrase and duet type sharing significantly decreased as distance increased between birds' territories (Fig. 4, Mantel test, $p < 0.05$). This pattern was observed across all years included in the analysis and within each individual year, with the exception of the year 2015, in which only female phrase type sharing was significantly correlated with distance (Fig. 4).

Repertoire stability across years

Individuals appear to use the same repertoire of phrase types throughout years when remaining in the same territory and with the same partner (Fig. 5). Overall, there were very few new phrase types recorded across different field seasons, and, in seven females and four males no different phrase types

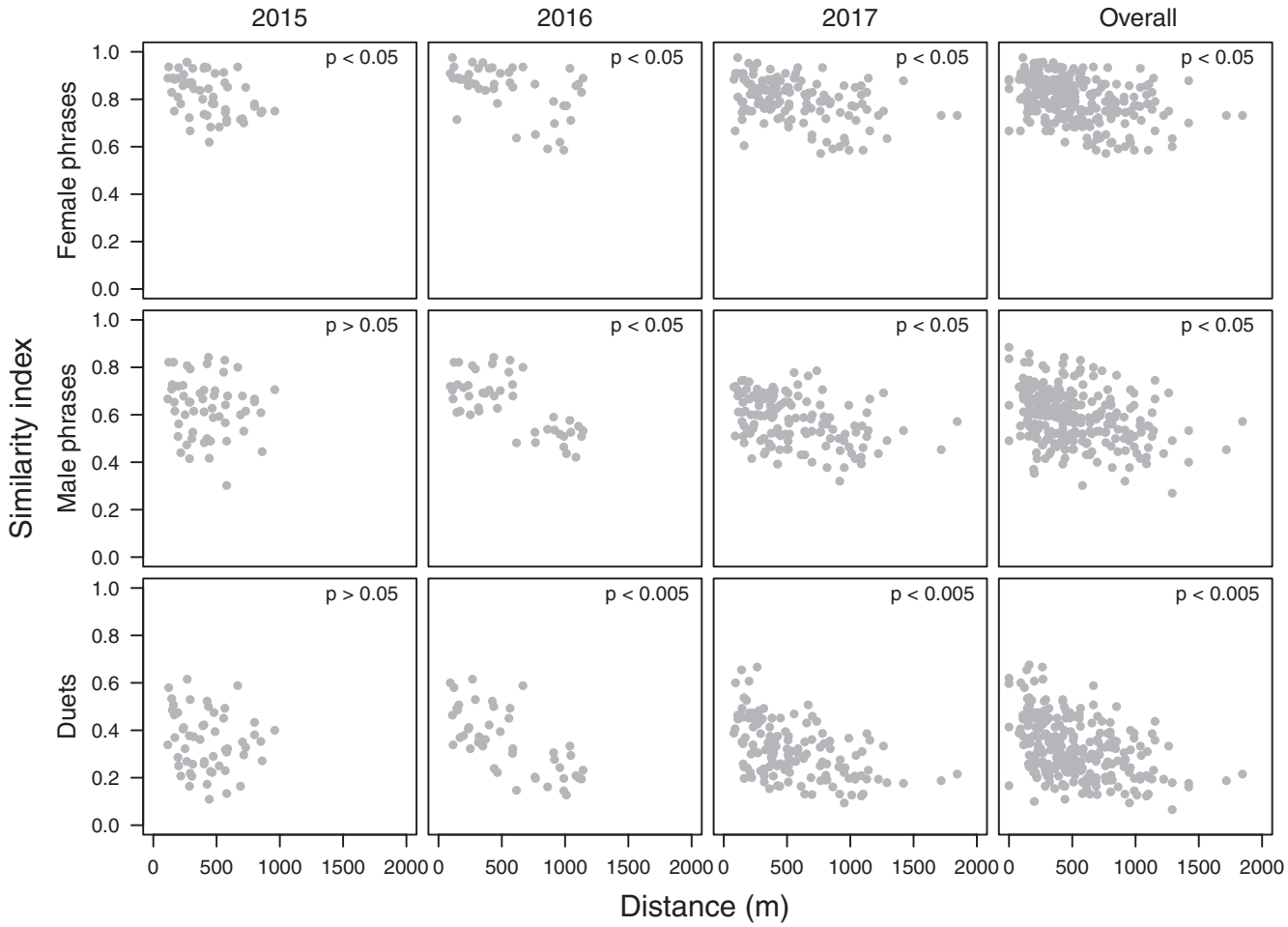

Figure 4. Phrase type and duet type sharing among females, males and pairs within the population in 2015, 2016, 2017 and the overall sharing taking in account all years sampled. The p-value was calculated based on 1000 permutations of rows and columns of the sharing matrix.

were found across years. Observed additions to individual repertoires were well within the expected range given by the 95% confidence interval around Chao-1 estimates, and close to zero for all 11 females and 11 males sampled (Fig. 5). Regarding duet types, pairs also tended to use the same duet type repertoires over time, and in two pairs no new duet types were recorded in different years despite significant recording effort (Fig. 5). In all 11 pairs sampled, duet type additions were also well within the expected range given by the confidence interval and very close to the Chao-1 estimate (Fig. 5). On average, across years, females sang $91 \pm 0.03\%$ (SE) of the same female phrase types, males sang $87 \pm 0.04\%$ of the same male phrase types and pairs sang $82 \pm 0.04\%$ of the same duet types.

Repertoire stability after remating events

Individuals that stayed in the territory (five females and three males) tended to use the same repertoire of phrase types even after changing partners (Fig. 6). However, three individuals (one male and two females) sang one or two additional phrase types over Chao-1's 95% credible interval, and yet another female sang four additional phrase types over the expected range (Fig. 6). As for the comparison between individuals that arrived (new mate) and left (previous mate) the focal territory, only one new mate (male) sang two additional phrase types over the expected range. Hence, individuals new to the territory used phrase type repertoires that were highly similar to the previous/replaced same-sex individual's repertoire (Fig. 6). On average, the birds that stayed in the territory sang $83 \pm 0.02\%$ (SE) of the same phrase types before and after remating, and the new individuals sang $78 \pm 0.05\%$ of the same phrase types as the same-sex replaced bird. Finally, regarding duet types, all eight of the newly formed pairs sang new duet types, with four pairs adding a small number of new duet types (that did not exceed the upper limit of the 95% confidence interval for the estimated new duet types), and four pairs adding significantly more new duet types than expected (Fig. 6). On average, new pairs sang $63 \pm 0.04\%$ of the same duet types as the previous pairs in the same territory. When comparing individuals that remained together and individuals that experienced a remating event, the difference

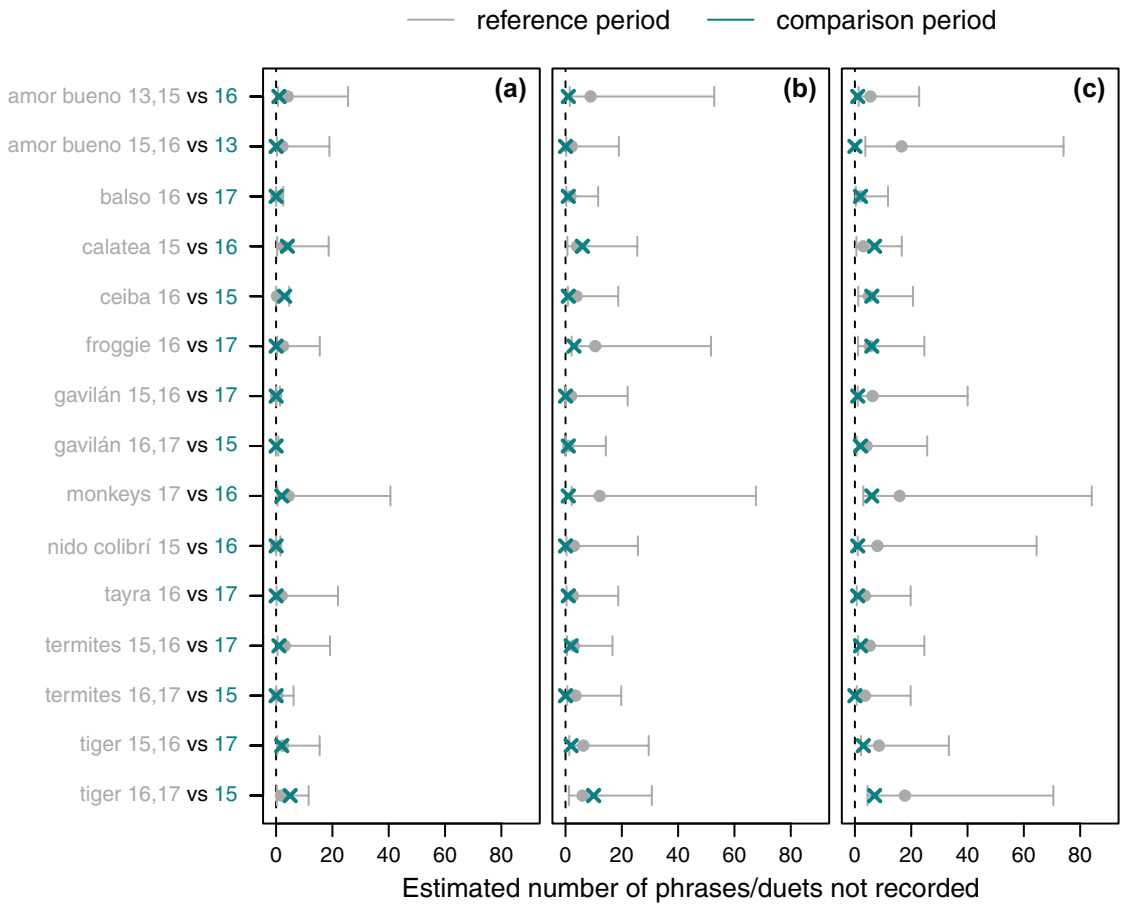

Figure 5. Number of different (a) female phrase types, (b) male phrase types and (c) duet types recorded in the comparison period (teal) that were not recorded in the reference period for each pair. Point estimates and the 95% confidence intervals of the reference period (grey) were obtained using the Chao-1 estimator, calculating the repertoire size that would have been obtained for that period if infinite songs had been recorded. Stability of phrase and duet types were evaluated by comparing the estimates from the reference period to the number of different phrase and duet types recorded in the comparison period. Values larger than the upper limit of the 95% confidence interval suggest innovation/lack of stability. Eleven pairs that stayed together for at least two years were used in this analysis, and if recorded in three different years, two comparisons were made, one combining the two first years and another combining the two last years.

between observed and expected new duet types was noticeably higher for the individuals that changed partners (Fig. 7).

Turnover rates and pair-bond length

We found a 60% annual turnover rate in this population of riverside wrens. From the 61 adult individuals banded and monitored during 2013–2017, 19 individuals were only seen in one year (ten females, nine males), 21 were seen across two years (ten females, eleven males), 16 across three years (eight females, eight males), 4 across four years (three males, one female), and only 1 (male) was seen across five years. Regarding pair-bond length, the majority of partnerships lasted approximately one year. From the 37 pairs in which both members were banded and monitored during 2013–2017, nine pairs were seen together in the same territory in two years, three pairs were seen together in three years, and one pair was seen together in four years, with none seen together more than that. In the 24 instances where a remating was recorded, in 13 cases it was the female which was no longer seen in the territory, in seven cases it was the male, and in four cases it was both pair members. Additionally, there were six remating instances that occurred while we were at the field site, allowing us to observe that territorial vacancies were filled within 48 h, with no lone territory holders being observed for longer than this time period. Finally, the birds that were re-sighted after a divorce and had left their previous territory (four males and two females), were found established only one or two territories away (70–150 m).

Discussion

Riverside wrens shared a considerable proportion of their phrase type repertoires with other same-sex individuals and a smaller proportion of their duet type repertoires with other pairs across the population. As previously seen in other tropical duetting birds (Levin 1996, Logue 2007, Rogers et al. 2007),

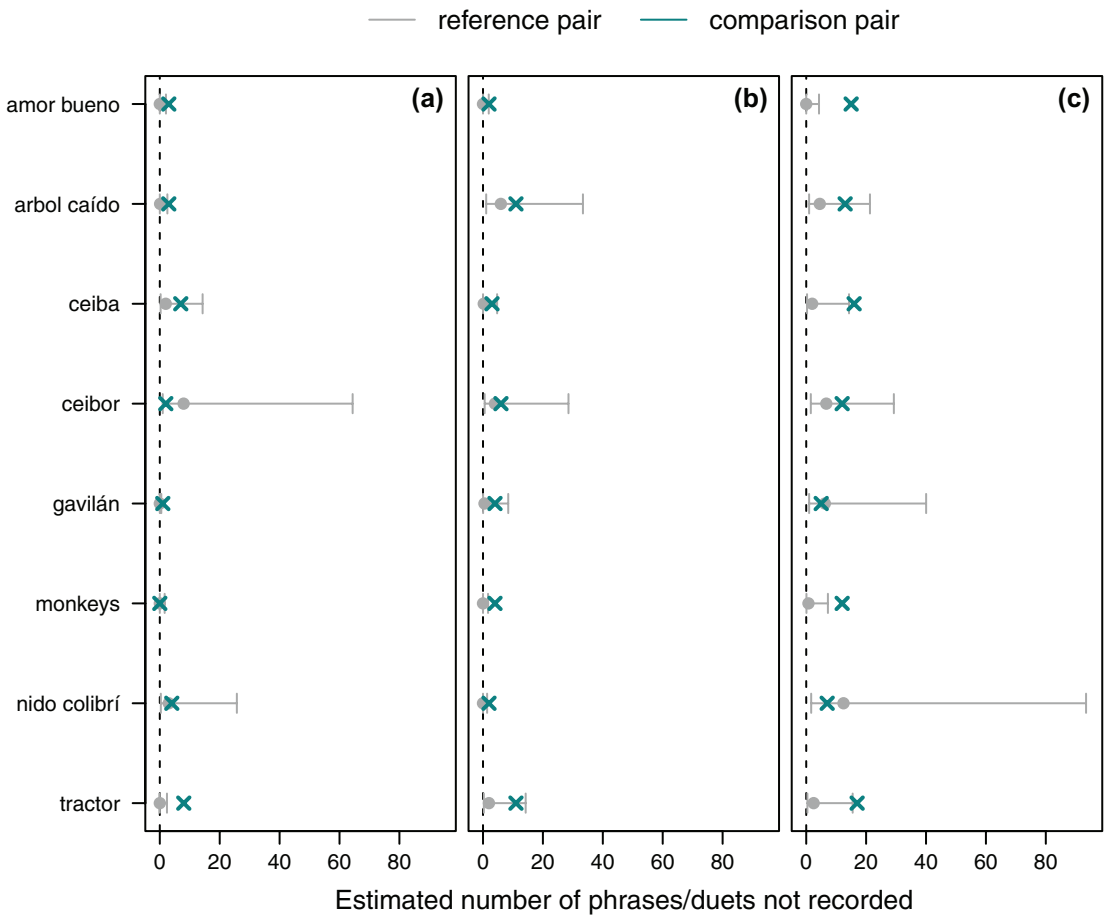

Figure 6. Number of different (a) phrase types of the individual that stayed, (b) phrase types of the new individual and (c) duet types of the new pair (teal) that were not recorded in the previous pair in each territory. Point estimates and the 95% confidence intervals of the reference pair (grey) were obtained using the Chao-1 estimator, calculating the repertoire size that would have been obtained for that pair if infinite songs had been recorded. Stability of phrase types and duet types were evaluated by comparing the estimates from the reference pair to the number of different phrase/duet types recorded in the comparison pair. Values larger than the upper limit of the 95% confidence interval suggest innovation/lack of stability.

females had smaller phrase type repertoires and higher sharing levels than males. Nevertheless, both sexes in this species had, on average, less than 1% of their repertoire comprised of unique phrase types. While sharing levels among immediate neighbours varied, there was a significant decline of shared phrase and duet types as distance increased between birds' territories. Furthermore, we found no evidence of individuals changing their phrase type repertoires over time or after remating, and duet code stability across years was also high when birds remained with the same mate in the same territory. Stability, however, was less consistent within individuals who changed mates. Although most birds maintained the majority of the duet types used with the previous partners, a few individuals changed a significant proportion of their previous duet type repertoire. Finally, we found a surprisingly high annual turnover rate in this population, with most pairs remaining together for no longer than one year.

The spatial patterns of song sharing found in this population were very consistent across sexes and across years: repertoire sharing gradually decreases with increasing distance between birds and there is considerable variation in the repertoire sharing levels among close neighbours. This pattern is expected in age-restricted learners that disperse nearby and settle next to their tutors unless no vacancies are available (Wilson et al. 2000). Given that almost all birds included in our study did not significantly change their individual phrase type repertoires over time or after changing partners, individual adult repertoires seem to be highly stable. Therefore, similar to slate-coloured boubous, *Laniarius funebris* (Wickler and Sonnenschein 1989), and African forest weavers, *Ploceus bicolor* (Seibt et al. 2002), both sexes in riverside wrens might create their individual repertoires as juveniles during a sensitive phase of development and thus present a close-ended learning strategy. The song sharing patterns also suggest that after juveniles leave their natal territory, both females and males remain nearby as floaters and attempt to settle in the vicinity. During the five years we studied this riverside wren population, we banded 18 juveniles on their natal territories.

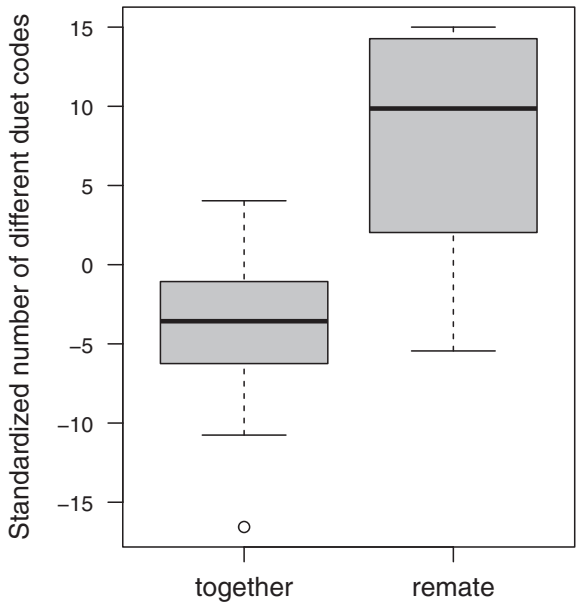

Figure 7. Average difference between observed and estimated number of different duet types not recorded in the reference period/pair. The number of observed different duet types were the number of duet types recorded in the comparison period/pair that were not recorded in the reference period/pair. The estimated number of different duet types was obtained using the Chao-1 estimator, calculating the repertoire size that would have been obtained in the reference period/pair if infinite duets had been recorded. Given that in some cases we over-estimated the repertoire size, the observed number of different duet types in the comparison period/pair were sometimes less that the estimated number of different duet types for the reference period/pair, resulting in a negative value.

Three were re-sighted as adults (two males and one female), and each settled only one or two territories away. Since the farthest territories within our field site are 2 km apart from each other, it is likely that we would have re-sighted birds within this entire area if they were present. Moreover, observations during fieldwork show that territory vacancies are occupied in less than 48 h after an individual is no longer in the territory, thus suggesting that floaters might be common in this population. In buff-breasted wrens, *Cantorchilus leucotis*, natal dispersal is also similar in both sexes, with juveniles moving only one or two territories away from their natal territory and most individuals therefore sharing territory borders with next of kin (Gill and Stutchbury 2006). There is, however, evidence of duetting species presenting sex-biased dispersal, such as in rufous-and-white wrens, *Thryophilus rufalbus*, where females move farther away than males and present lower song sharing between neighbours (Graham et al. 2017). Given that males in our study had lower song sharing levels than females, increasing the sample size of recruited juveniles in the future will enhance our understanding of how dispersal shapes the song sharing patterns found in this species.

Regarding duet code stability, we found that pairs that stayed together in the same territory did not change their duet type repertoires across years, as seen in eastern whipbirds, *Psophodes olivaceus* (Rogers 2005), and black-bellied wrens, *Pheugopedius fascioventris* (Logue 2006). However, adult riverside wrens showed a high turnover rate, especially unusual for a tropical species (Freed 1987, Stutchbury and Morton 2001, Green et al. 2004, Gill and Stutchbury 2006, but see Levin 1996, Logue 2007). Hence, after natural mate changes, either by divorce or death, birds that stay in the territory have to create a duet code with the new mate. Given that duet types involve a combination of both members' individual repertoires, new duet types are expected if the new partner has different phrase types from the replaced partner. In a study with bay wrens in which individuals were forced to change partners, even though females did not change their individual repertoires, their pair repertoires drastically changed because the new males had completely different phrase type repertoires (Levin 1996). Consistent with this, we found that birds that stayed in the territory used phrase types from their individual repertoire to create new duet types with the new phrase types of the new mate.

As for the phrase types that were shared between the previous and new mate, most duet types of the new pair were comprised of the same associations of phrases as the previous pair. In bay wrens and canebrake wrens, most individuals also retained the same rules for associating their own phrases with the shared phrases between the previous and new mate (Levin 1996, Rivera-Cáceres et al. 2016). Nonetheless, we also documented several new duet types in which the individual that stayed in the territory used a different phrase type in response to a previously known phrase type of the opposite sex. As Rivera-Cáceres et al. (2016) suggested, it is likely that in order to include a duet type into a pair's repertoire, both members of a pair have to 'agree' on the combination of their individual phrase types to consistently associate those same phrases together. Otherwise, the individual that does not 'agree' with the duet type can either stop singing in response to its partner or switch phrase types (Rivera-Cáceres et al. 2016).

Even though some newly formed pairs created new duet types, our findings suggest that most individuals maintain a considerable portion of their duet type repertoire throughout their lives. During our study, in all six instances in which we re-sighted adult birds that changed territory, we found them re-established only one or two territories away, rather than in more distant locations. If both females and males remain in the vicinity after a divorce, such behaviour might explain why previous and new partners share such a high proportion of their same-sex phrase type repertoires, and also why previous and new pairs in the same territory share a large proportion of their duet type repertoires, noticeably more than between neighbouring pairs, and substantially more than with all pairs across the population. It is therefore possible that the high levels of duet code sharing observed in riverside wrens are also the result of their delayed and limited dispersal. Given that juveniles remain with their parents for several months (Skutch 2001, Esmeralda Quiros-Guerrero unpubl.), they might not only learn the phrase types but also the duet types sung by their parents and neighbouring tutors. During our study,

we have recorded juveniles singing highly developed songs alongside their parents following their duet code, which suggests parents are indeed vocal tutors of their offspring. This has also been documented in superb-fairy wrens, *Malurus cyaneus*, where fledglings acquire song elements from their mothers and social fathers (Evans and Kleindorfer 2016), and in canebrake wrens, where juveniles improved their temporal coordination and duet code adherence while duetting with their parents over time (Rivera-Cáceres et al. 2018).

An alternative explanation for the high levels of phrase and duet type sharing documented in this study could be that repertoire sharing allows individuals and pairs to song match or repertoire match in order to escalate or de-escalate aggression during agonistic interactions (Nordby et al. 1999, Beecher and Brenowitz 2005). In an experiment investigating phrase type sharing in male banded wrens, *Thryothorus pleurostictus*, a species with high levels of repertoire sharing, males were considered more aggressive when using shared or matching phrase types than when using unshared or non-matching phrase types (Molles and Vehrencamp 2001). Additionally, in canebrake wrens, females and males phrase type matched the playback more often than expected by chance, suggesting phrase type matching could indeed have an intrasexual aggressive dynamic in this species (Marshall-Ball and Slater 2004). Therefore, it is possible that in riverside wrens, sexual selection also influences the song sharing patterns found in this study, with phrase type matching playing an important role in intrasexual communication in both sexes. Given the high turnover rate observed in this species, having a high proportion of shared phrase and duet types could facilitate communicating with neighbours without having to learn a new repertoire every time an individual in the vicinity changes.

In conclusion, contrary to initial predictions, this study provides evidence of a high turnover rate in a neotropical species with pair-specific repertoires of duet types. This suggests that long-term partnerships are not necessary to develop duet codes in duetting birds. In riverside wrens, limited dispersal and imitation are likely to be driving the song sharing patterns and repertoire stability found, despite the high turnover rates observed. Future work will investigate counter-singing dynamics between individuals and between pairs during the dawn chorus and during playback experiments to increase our understanding of how phrase types and duet types are used in between-pair interactions in duetting species.

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